

Extra-pair paternity in a long-distance migratory songbird beyond neighbors' borders and across male age classes

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Abstract: Roughly 90% of socially monogamous bird species exhibit some degree of extra-pair paternity (EPP), although the extent and the underlying mechanisms vary among species. We analyzed spatial and demographic patterns of EPP over a 6 year period (2005–2010) as part of a long-term population study of Canada Warblers (*Cardellina canadensis* (L., 1766)). We identified 12 microsatellite loci used to assess paternity for 185 nestlings from 61 nests. Extra-pair young (EPY) accounted for 41.6% of all nestlings and 57.4% of nests contained at least one EPY. Fewer than half of EPY were sired by males who shared territorial boundaries, and some males sired young in nests 1 km from their territory. The age of social males did not differ from males who cuckolded them. The majority (83%) of EPY were sired by males in older age classes (2+ years old), while <17% were sired by 1 year olds. Of the young sired by older males, 58.5% were sired by males 3–7 years old. Males that sired more EPY sired fewer within-pair young (WPY); those without EPY sired more WPY suggesting a possible fitness trade-off between these two strategies. Our findings suggest multiple age-based strategies within a single breeding population, as well as potential strategy shifts to maximize lifetime fitness as they age.

Key words: Canada Warbler, *Cardellina canadensis*, within-pair paternity, lifetime fitness.

Résumé : Un certain degré de paternité hors couple (PHC) caractérise environ 90 % des espèces d'oiseaux monogames sur le plan social, bien que l'ampleur de ce phénomène et les mécanismes sous-jacents varient d'une espèce à l'autre. Nous avons analysé les motifs spatiaux et démographiques de PHC pendant 6 ans (2005–2010) dans le cadre d'une étude de longue durée de populations de parulines du Canada (*Cardellina canadensis* (L., 1766)). Nous avons cerné 12 sites microsatellites utilisés pour évaluer la paternité de 185 oiseaux nés de 61 nids. Les jeunes de paternité hors couple (JHC) représentaient 41,6 % de tous les oiseaux nés et 57,4 % des nids contenaient au moins un JHC. Moins de la moitié des JHC étaient issus de mâles partageant des limites territoriales, et certains mâles avaient une progéniture dans des nids situés à 1 km de leur territoire. L'âge des mâles sociaux n'était pas différent de celui des mâles qui les couvaient. La majorité (83 %) des JHC étaient issus de mâles de classes d'âge plus vieilles (2 ans et plus), alors que <17 % étaient issus de mâles de 1 an. Parmi les jeunes issus de mâles plus vieux, 58,5 % étaient issus de mâles âgés de 3 à 7 ans. Les mâles qui engendraient plus de JHC engendraient moins de jeunes au sein du couple (JSC); ceux sans JHC produisaient plus de JSC, ce qui indiquerait un possible compromis sur le plan de l'aptitude entre ces deux stratégies. Nos résultats semblent indiquer l'adoption de différentes stratégies selon l'âge au sein d'une même population reproductrice et de possibles changements de stratégies au fil du vieillissement afin de maximiser l'aptitude sur la durée de vie. [Traduit par la Rédaction]

Mots-clés : paruline du Canada, *Cardellina canadensis*, paternité au sein du couple, aptitude sur la durée de vie.

Introduction

Extra-pair paternity (EPP) is common among socially monogamous bird species with approximately 90% of socially monogamous species exhibiting some degree of EPP (Griffith et al. 2002), and this behavior has potentially strong fitness consequences (Birkhead and Møller 1998). Siring young outside a social pair bond has the ability to enhance productivity within a single breeding season and is an important component of male fitness (Griffith et al. 2002, Kaiser et al. 2015), but males within a population can differ considerably in their fitness gains from EPP (Sardell et al. 2010; Reid et al. 2014; Kaiser et al. 2015).

Territory location, habitat quality, and age have been shown to influence EPP (Woollfenden et al. 2005; Sardell et al. 2010; Kaiser et al. 2015). Older males generally rank higher in the social hierarchy and thus perform better by asserting competitive domi-

nance (Hunt 1996; Marra and Holmes 2001; Reitsma et al. 2008). Therefore, an individual's energy allocation toward seeking EPP may be influenced by experience. Long-term studies offer some resolution on whether the proclivity toward EPP relates to an individual's changing priorities associated with age-specific benefits and constraints (Sardell et al. 2010). Tracking the cumulative fitness of individuals of known age throughout their life can add significant insight into how reproductive strategies change with age.

Long-distance migrants tend to have shorter breeding seasons, which increases nesting synchrony, thereby enhancing the opportunity for EPP (Spottiswoode and Møller 2004), although this hypothesis has mixed support (Stutchbury 1998; but see Weatherhead and Yezerinac 1998). We used a long-distance migratory songbird, the Canada Warbler (*Cardellina canadensis* (L., 1766)), to identify how mating strategies change with age class. The Canada Warbler is a

Received 6 November 2016. Accepted 2 July 2017.

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Table 1. Age composition of the male Canada Warbler (*Cardellina canadensis*) populations in each of the 4 years with an adequate number of nests analyzed and beginning in the year that individuals could be in the oldest age category given when these populations were first aged.

Year	Age (years)			
	1	2	3	≥4
2007	10	19	8	5
2008	5	10	14	11
2009	15	6	5	12
2010	8	10	2	14

Note: Only 9.8% ($n = 6$) of males in these analyses were from 2005 and 2006 when minimum ages could not have exceeded 2 and 3 years, respectively.

long-distance, obligate single-brooded migratory songbird with relatively high nesting synchrony. We measured reproductive output of individuals within a breeding population in New Hampshire, USA, as part of a long-term population study to test whether EPP is consistent across age classes. We performed genetic parentage analyses for nestlings studied over six consecutive years. Having documented higher nesting success among older males (Reitsma et al. 2008), we predicted that they would also sire more extra-pair young (EPY) because of their greater experience in defending territories and attracting mates (Cleasby and Nakagawa 2012). This species breeds in forested wetlands with high stem densities and complex ground cover. Populations at landscape scales are patchily distributed in accordance with their suitable habitat consisting of “clusters” of territories (hereafter neighborhoods) that vary in size contingent upon habitat structure (Hallworth et al. 2008a). Based on the clumped dispersion documented by Hallworth et al. (2008b), we predicted greater EPY among males within the same neighborhoods, specifically among adjacent territorial males.

Materials and methods

Study site

The study area in Canaan, New Hampshire, USA (43°40'N, 72°03'W), encompasses ~450 ha with a centrally located bog separating two study sites each with distinct habitat features (Hallworth et al. 2008a). For a detailed description of the study area see Hallworth et al. (2008a, 2008b) and Reitsma et al. (2008). The study area south of the bog is a relatively level red maple (*Acer rubrum* L.) swamp interspersed with mixed deciduous–coniferous sections with a taller canopy and lower stem density. The study area north of the bog varies in elevation with early to mid-successional forest dominated by the same species as the plot south of the bog. This area is interspersed with higher, drier forest and small boggy areas with mossy ground cover and persistent standing water. Both study areas have been studied without interruption since 2005 and have had consistently high annual return rates, pairing, and fledging success (Hallworth et al. 2008b; Reitsma et al. 2008).

Territory mapping

During the 2005–2010 breeding seasons, male Canada Warblers were captured and uniquely color-banded for later identification ($n = 118$ individuals). Upon capture, each male was aged (Table 1) using plumage characteristics (distinctive molt limits; Pyle 1997). We captured fewer females ($n = 36$) because they do not respond to playback and we did not attempt captures at nests. Of those males breeding for the first time in the study area, 60.5% were after

second year (ASY) males, and we assigned them a conservative age of 2, the minimum age possible. All males in a given breeding season were assigned to age classes ranging from 1 to 7 years old. For example, an unbanded male with second year (SY) plumage was assigned the age of 1 year old and an unbanded male with ASY plumage was assigned the age of 2 years old. Individuals who were captured and initially aged as ASY and returned were aged as 3 years old.

From 2005 to 2007, we mapped male locations using handheld Global Positioning System (GPS) devices following the protocol reported in Hallworth et al. (2008b), in which color-banded males were followed and locations were marked at 5 min intervals without influencing their behavior. During the breeding season 2008–2010 at least 36 (57.28 ± 16.74 ; mean \pm 1 SD) locations per individual in each year were obtained opportunistically during territory visits, as opposed to the 42 minimum in prior years. Male territories were generated using kernel density estimates (KDE), which were calculated in the program R version 3.2.0 (R Core Team 2013). We used least-square cross validation to estimate the bandwidth or smoothing parameter (Barg et al. 2005). We used the territory centroid, the center location of the 95% KDE, and measured distances between these centroids to determine the distance from other males within the population. We searched for nests while mapping territories, and when nests were found ($n = 117$), we banded nestlings to quantify natal philopatry, obtained a blood sample, and estimated nestling age or noted hatching dates. We considered males to be social males if they were observed feeding young and (or) the nest was placed within their respective territory. Boundaries are known to shift early in the season before all males arrive but thereafter remain stable until fledging (L.R. Reitsma, personal observation).

Genetic analysis

We collected DNA samples from Canada Warbler nestlings ($n = 185$ with confident paternity assignment), as well as breeding males and females, and identified microsatellite loci useful for performing parentage analysis. Blood was stored in Queen's lysis buffer (Seutin et al. 1991) and transported to the laboratory where it was stored at -20°C . DNA was extracted using the Qiagen DNeasy blood and tissue kit according to the manufacturer's instructions. Samples were eluted in buffer AE and DNA concentrations were determined using a Nanodrop ND-1000 spectrophotometer. We tested many primer sets (data not shown) and identified 15 polymorphic microsatellite loci that were used for further paternity analysis. Six of our loci were developed specifically for the Canada Warbler by screening a microsatellite-enriched genomic cDNA library according to the methods described by Glenn and Schable (2005). The remaining nine were developed for other avian species (Supplementary Table S1),¹ but amplified putatively orthologous microsatellite loci in the Canada Warblers. We scored individual genotypes by amplifying genomic DNA from individual birds (100–200 ng) in a 10 μL reaction containing 1 μL 10 \times polymerase chain reaction (PCR) buffer, 1.5–2.0 mmol/L MgCl_2 , 0.5 U *Taq* polymerase (New England Biolabs), 0.5 $\mu\text{mol/L}$ of each primer, and 100 $\mu\text{mol/L}$ dNTPs. PCR cycling conditions are listed in Supplementary Table S1.¹ One primer from each locus was fluorescently labeled for multiplex fragment analysis. PCR products were diluted and mixed with formamide and GeneScanTM 500 ROXTM size standards (Life Technologies). PCR fragments were sized in 10 μL multiplexed samples on an ABI 3100 Genetic Analyzer (Applied Biosystems) at the Dartmouth College Molecular Biology Core Facility. Allele sizes of PCR fragments were calibrated with an internal size standard and scored using Genescan version 3.0 software (Applied Biosystems). Data were manually checked for scoring accuracy.

¹Supplementary table is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0277>.

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Fig. 2. The number of extra-pair young and within-pair young in each Canada Warbler (*Cardellina canadensis*) nest. Slopes for each age class are represented along with the mean of all age classes combined.

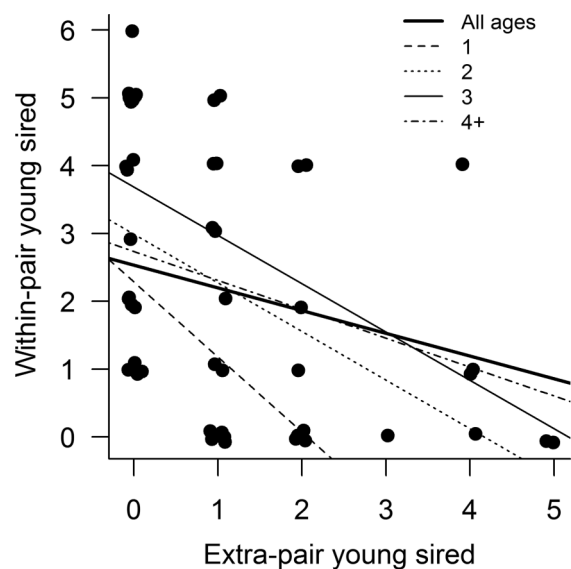
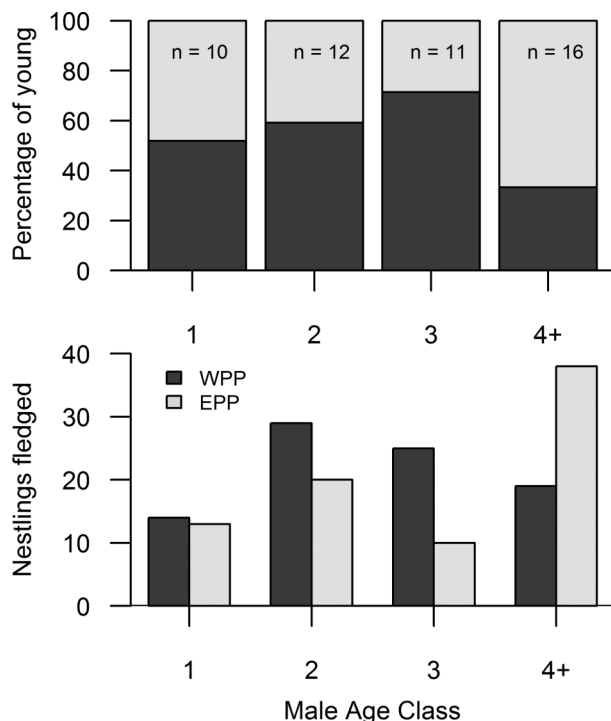
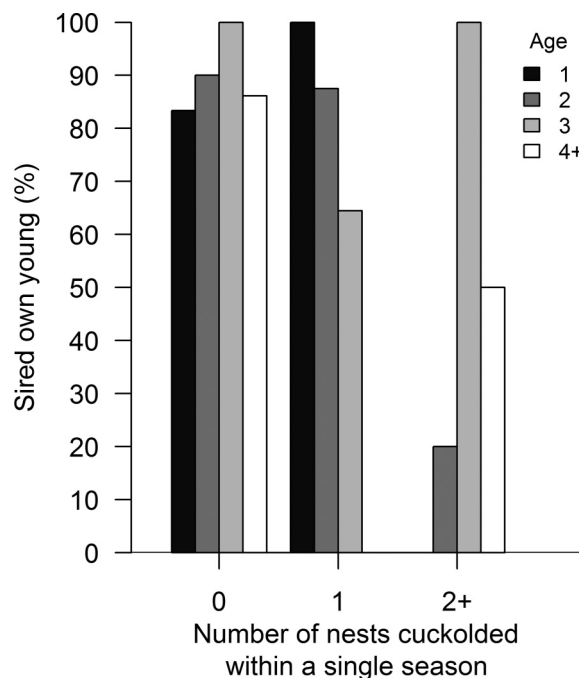


Fig. 3. The percentage of within-pair young (WPY) and extra-pair young (EPY) Canada Warblers (*Cardellina canadensis*) produced within the four age classes over the duration of the study, from 2005 to 2010 (top panel). The total number of WPY and EPY within the four age classes over the duration of the study (bottom panel).



EPY ($n = 26$) sired at least 1 WPY with the exception of one male. In contrast, males that sired EPY in multiple nests within a season ($n = 10$) had a lower incidence of siring WPY (Fig. 4). Males with EPY in one nest ($N = 27$) were intermediate between the previous two groups. Males with the highest cumulative number of nests with EPY ($n = 5$ nests) had the highest ratio of EPY to WPY (4:1). That ratio dropped to 1.4:1 for males that cuckolded four nests over the years included in this analysis. Males that sired EPY young in two

Fig. 4. Within-pair paternity (WPY) was verified for all but 1 of 26 Canada Warbler (*Cardellina canadensis*) males that had no documented extra-pair young (EPY), whereas 40.7% of males with EPY in one nest had WPY and only 20% of extra-pair males with EPY in two or more nests in a single season had documented WPY. The percent totals are across all age classes within each category of number of nests cuckolded.



and three nests had EPY to WPY ratios of 0.77:1 and 0.87:1, respectively. Males that cuckolded only one nest had a ratio of 1.18:1 and represented 41.7% of all males with EPY. The ratios reported here are conservative estimates because males were excluded from these analyses if the social nest was not found in the year where the EPY that he had sired were documented.

Discussion

Canada Warblers, a single brooded, long-distance migratory songbird, exhibited comparatively high rates of EPP compared with other migratory passerines. Male age class was an important, though not statistically significant, factor in determining the number of young sired outside of the social pair bond. The oldest males (4+ years old) sired more EPY than younger males (<4 years old) but at the possible cost of siring fewer WPY (see Cleasby and Nakagawa 2012). Our analyses of age effects are conservative. We included males assigned the age of 2 if caught as ASY males in their first breeding season on these study sites and thus the actual age of these individuals is likely to be older than the age that we assigned. Males were cuckolded by individuals beyond those who shared a territory boundary. Social males were sometimes cuckolded by males with territories 1 to 2+ km from their territory, documenting extra-pair forays to territories beyond neighbors, even to other neighborhoods. Despite longer forays, EPP declined with increasing distance from male territory similar to Black-throated Blue Warblers (*Setophaga caerulescens* (J.F. Gmelin, 1789)) but on a smaller spatial scale (Kaiser et al. 2017).

The incidence of EPY (41.6%) reported here for Canada Warbler is comparable with other species of migratory woodland warblers breeding within the region. Black-throated Blue Warblers (35.1% EPY), another Nearctic–Neotropical migrant reported from a site about 60 km northeast of our study area (Kaiser et al. 2015), and Hooded Warblers (*Setophaga citrina* (Boddaert, 1783)) (34% EPY)

breeding in deciduous forests of Pennsylvania, USA (Chiver et al. 2008), migrate similar distances, about half that of the Canada Warbler. As such, these species have the opportunity to double brood, whereas the latter is an obligate single-brooded species (Reitsma et al. 2010). In contrast, a nonmigratory insular population of Song Sparrows (*Melospiza melodia* (A. Wilson, 1810)) had an overall EPP rate of 28% (Sardell et al. 2010).

This study may elucidate further links between EPP and life-history traits, such as distance migrated, number of broods, and breeding synchrony, that suggest a higher rate of EPY among longer distance migrants.

Our findings elucidate age-specific reproductive strategies that can only be identified through long-term population studies. We found that male age is important in determining which individuals sire EPY. Age has been found to be positively correlated with EPY but not WPY in other passerines as well, such as Mountain Bluebirds (*Sialia currucoides* (Bechstein, 1798)) (Balenger et al. 2009), Reed Buntings (*Emberiza schoeniclus* (L., 1758)) (Kleven et al. 2006), European Pied Flycatchers (*Ficedula hypoleuca* (Pallas, 1764)) (Lehtonen et al. 2009), and Splendid Fairy-wrens (*Malurus splendens* (Quoy and Gaimard, 1830)) (Webster et al. 2007). Our results are similar in that we found no relationship between age and WPY, but the oldest age classes had higher rates of EPY. Older males may have a greater opportunity to seek extra-pair copulations because they arrive and establish social bonds with females earlier than young males, thus allowing older males to seek extra-pair copulations after their mates initiate the earliest incubation (Reitsma et al. 2008; Kaiser et al. 2017). Although males that were 1 or 2 years old were responsible for 41.6% of all EPY, the higher EPY to WPY ratio of males 4 years old or older suggests experience contributes to the number of EPY sired within a single season. Although experience likely plays a role in the number of EPY sired, the underlying mechanism for the relationship between rates of EPP and male age needs further study (Kleven et al. 2006; Webster et al. 2007; Lehtonen et al. 2009). Our results suggest reproductive strategies may shift in the oldest age classes.

Territory dispersion has been shown to contribute to paternity patterns (Norris and Stutchbury 2001; Woolfenden et al. 2005; Kaiser et al. 2015). Habitat specialists occupying isolated patches (Hallworth et al. 2008b), linear strips (Woolfenden et al. 2005), or fragmented landscapes (Norris and Stutchbury 2001) may be compelled to foray farther distances from territories to secure EPY. Canada Warbler neighborhoods occur in suitable dense and wet habitat with interspersed lower stem density and drier forest (Hallworth et al. 2008a). Thus, one advantage Canada Warblers may have in long-distance forays is remaining within forested habitat. EPY were not restricted to neighbors with six instances of nestlings sired by males greater than 1 km from their respective territories in 2008 alone. In this regard, they more closely resemble Hooded Warblers (Norris and Stutchbury 2001) and Acadian Flycatchers (*Empidonax virens* (Vieillot, 1818)) (Woolfenden et al. 2005), species that sire young across large distances due to willingness to foray among fragments or having linearly arranged territories, respectively. EPY may, however, result from early phases of the breeding season when females are scouting and males occupy larger areas until future neighbors arrive (L.R. Reitsma, unpublished data).

Females may select varying phenotypes among males within the population or features of the habitat associated with individual males. Female Hooded Warblers, for example, use song as opposed to plumage characteristics when selecting males for extra-pair copulations (Chiver et al. 2008). Canada Warblers have variation in song repertoire with two distinct song modes (Demko et al. 2013). Song-sharing within the population has also been documented where newcomers switch element structure and their frequency range to adjust to neighbors (Demko et al. 2016). However, we did not concurrently measure EPP and song characteristics in our population. EPP is thought to drive sexual selection

of plumage characteristics in Splendid Fairy-wrens (Webster et al. 2007), European Pied Flycatchers (Lehtonen et al. 2009), and Mountain Bluebirds (Balenger et al. 2009) and plumage varies among male Canada Warblers even within age cohorts. However, we did not investigate whether plumage characteristics, such as the length of a male's necklace, relate to EPP success. Further research is needed to elucidate mechanisms of female choice for EPP in the Canada Warbler.

Our findings suggest that there is a fitness trade-off for siring EPY by compromising the number of WPY sired (see Fig. 2). The ratio of EPY to WPY was lower for males who cuckolded fewer nests, but potentially less so for the oldest males (lowest slope in Fig. 2). Maximizing EPY may come at the expense of siring or fledging WPY in part due to lower mate guarding (Westneat et al. 1990; Kaiser et al. 2015). This trade-off may be exacerbated for species with highly synchronized breeding attempts that do not double brood. Although outside the scope of the current study, males may seek to increase fitness through EPP as they age, instead of investing at their social nest. These two behaviors have been shown to be inversely related in other studies (Tuttle 2003; Clotfelter et al. 2007). We did not compare visitation rates among males of different age classes to explicitly test this hypothesis.

The long-term nature of this study provides insights into age-related performance that can only be revealed through a more detailed examination of advanced age classes. Having a complete profile (all EPY and WPY fledged) of each male in each year would provide a more robust measure of whether this species generally undergoes a shift in reproductive strategies with age (as in Song Sparrows; Sardell et al. 2010). However, we did track individuals over multiple years and our findings offer important contributions suggesting a possible shift in reproductive strategies with age in this socially monogamous species.

Canada Warbler males foray across extensive forested-habitat mosaics that include patches of their preferred habitat and areas not suitable for breeding. Genetic contributions of males greater than 2 km from their own nests suggest neighborhoods in discrete habitat patches may have frequent genetic exchange. Thus, maintaining a mosaic of intact habitat may ensure occupancy and facilitate gene flow among far-ranging Canada Warbler neighborhoods. These mosaics may be more likely to have diverse age classes with the requisite variation in documented reproductive strategies that likely contributes to the high reproductive success in this study area.

Acknowledgements

We thank P. Benham, J. Wampler, and A. Demko for assistance in data collection. We thank the Town of Canaan, New Hampshire, USA, and the Mascoma Watershed Conservation Council for permission to use the study sites. We thank P. Benham and the anonymous reviewers for critical reviews that improved the manuscript. This research was supported by the New England Institute for Landscape Ecology, Plymouth State University, the Mascoma Watershed Conservation Council, the Davis Conservation Fund, and the Charles E. and Edna T. Brundage Scientific and Wildlife Conservation Foundation. All tissue sampling followed protocols set by the U.S. Geological Survey (Bird Banding Laboratory). All procedures were in accordance with Plymouth State University's Institutional Animal Care and Use Committee regulations.

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